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The Reproductive System of the Army-Ant Queen, *Eciton (Eciton)*

Part 2. Histology

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Part 1 of this series of papers[2] described the general anatomy of the reproductive system of the army-ant queen. In this present part some information is furnished on the tissues of the organs and parts described in part 1.

THE VAGINA: The vagina is a stout, rounded duct connecting the vulva posteriorly with the anteriorly situated median oviduct. From the evidence available, the posterior end of the vagina serves as a copulatory pouch or bursa. A short distance from its posterior opening, the spermathecal duct originates dorsally and runs anteriorly to the spermatheca. There are apparently no other organs connected with it (fig. 1).

The lumen is lined with a very thick cuticula which exhibits both stout and delicate setae from the vulva to a point slightly anterior to the branching of the spermathecal duct. At the lower end, the epithelium (hypodermis) is either absent or sparsely represented by an occasional compressed cell. Most of the space one would assume to be occupied by the surface epithelium is in fact filled by muscle endings the fibrillae of which penetrate the endocuticula and extend to the exocuticula for an-

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[2] Hagan (1954). The three studies of which this is the second have been carried out in collaboration with the Department of Animal Behavior of the American Museum of Natural History. The writer wishes to express his thanks to Dr. T. C. Schneirla, Curator in that department, for having made available a series of queens collected and preserved by him in connection with his field investigations on army-ant behavior and biology. Each queen referred to in this study will be identified by the annual series and symbol used for her colony in the original publication (Schneirla, 1947; Schneirla and Brown, 1950).

chorage. Farther up the vagina the epithelium is entire and consists of cuboidal cells with ovate nuclei. A basement membrane is present although delicate.

The muscles at the lower end of the vagina, the ends of which replace the epithelium, all turn obliquely forward along the wall of the vagina outside a single layer of circular muscles. The latter is a fenestrated layer owing to the numerous insertions of the oblique muscles. The oblique muscles are numerous and prominent. From their position it is apparent that they are powerful dilator muscles which regulate the distention of the vagina in diameter. They also serve to contract in length the posterior portion of the vagina.

Anterior to the position just described, the rest of the vagina possesses an intima, epithelium, three layers of circular muscles, and, it is thought, occasional longitudinal muscles, though the last was not definitely determined. There are internal longitudinal folds involving only the epithelium, its basement membrane, and the cuticular intima. With the material at hand it was impossible to distinguish clearly between the vagina and the oviduct at their junction or to determine the former's length.

THE MEDIAN OVIDUCT: An apparent distinction to be made between the median oviduct and the vagina is that the latter is usually ovate in section or flattened dorsoventrally in the older queens while the oviduct is ovate or round. A second difference is in the thicker band of vaginal circular muscles which consists usually of three layers of cells, and in the addition of longitudinal muscles, though this last difference seems not to be constant for the entire length of the vagina. On the other hand, the epithelial folds surrounding the lumen of the oviduct, with the intima, are more numerous and the wall appears thinner than that of the oviduct in the virgin female. A portion of the oviduct wall in a virgin queen is shown in figure 2. The wall of the same structure in the older queen closely resembles the paired oviduct (fig. 3), but of course it possesses a cuticula.

THE PAIRED OVIDUCT: These oviducts are surrounded only by circular muscles. The epithelium next to the lumen gives rise to no cuticula. They are more delicate tubes than the median oviduct and vary greatly in diameter as was mentioned in part 1 (Hagan, 1954). Along the upper, exceedingly narrow portion of these ducts the circular muscles are very thin, consisting of only one cell layer (figs. 3, 4). This is true also for the extreme upper ends of these ducts where they enlarge again in diameter to join the calyx. Moreover, while the major portion of the paired oviducts is always tubular or only slightly oval, the expanded upper end

is severely flattened, so that in section the lumen is revealed as a broad slit.

The calyx is characterized by having a columnar epithelium which often appears cuboidal around the openings leading from the ovarioles. No basement membrane or lateral cell membranes could be detected nor do muscles seem to be present (figs. 8, 9).

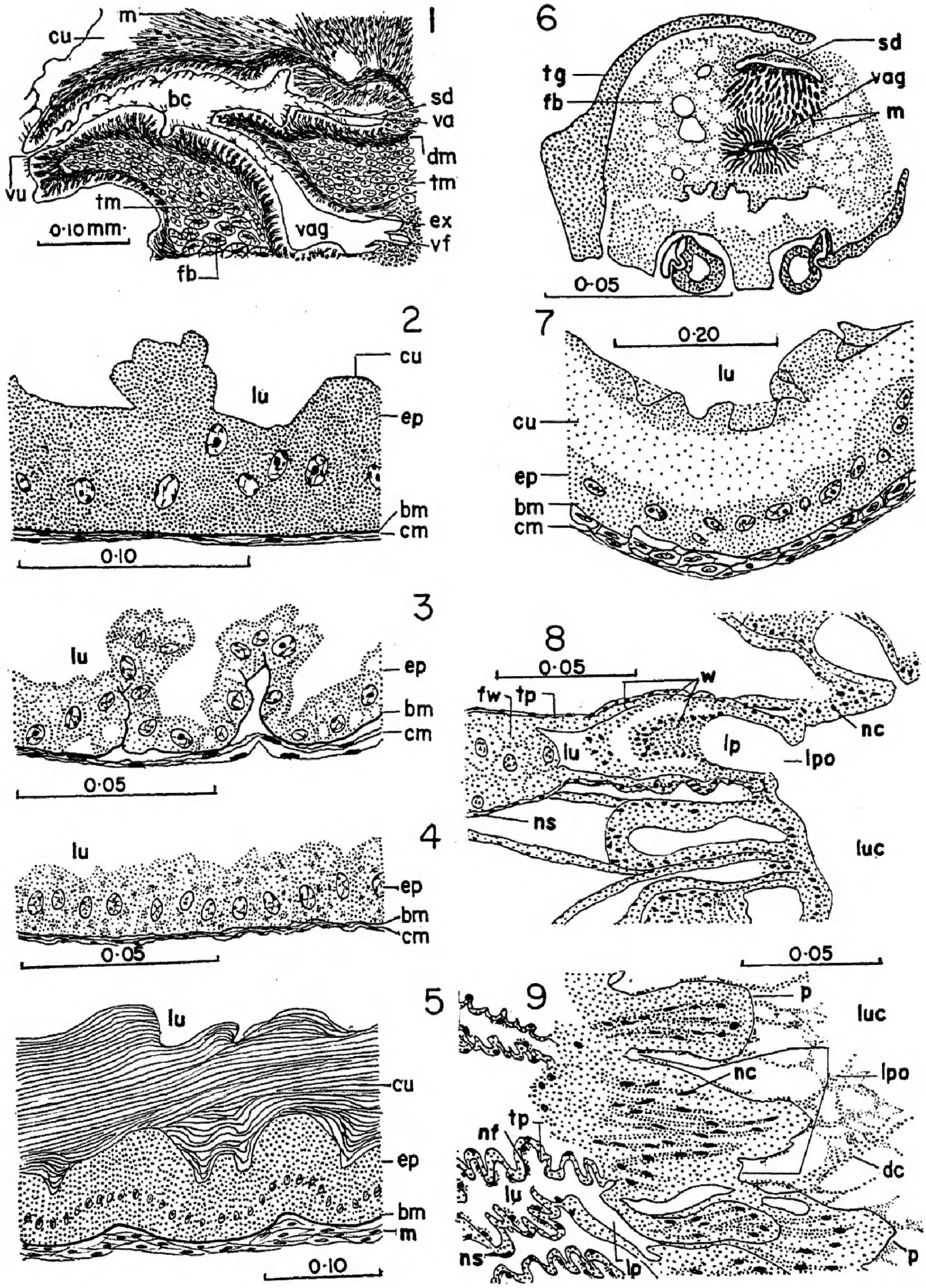
The structural arrangement of the virgin queen's calyx is simpler and easier to understand (fig. 8). This is probably because functional complexity has not appeared. It will be seen in figure 8 that the epithelium is rather uniformly smooth around the lumen except for the openings of the pedicel of each ovariole. One such opening and parts of three more are represented.

By way of contrast, a portion of the calyx of an older, functional queen is shown in figure 9. Traces of four or five openings to ovarioles are visible. It is at once apparent that the epithelium has been thrown into folds protruding into the lumen, and the surface surrounding the latter is quite rough and irregular. Further, the columnar shape of the epithelial cells is more pronounced, with the cytoplasm showing dense granular condensations near the central, long axis of the cells.

Approximately 1200 ovarioles open independently into the calyx, but the openings, together with a portion of the lumen of the ovariole, are difficult to find, especially in the functional queen. The pedicel of the ovariole opens on the general surface or in a slight depression in the calyx of the virgin queen. In the case of the functional queen, however, this opening is invariably at the inner end of a deep depression or evagination of the calyx wall. The epithelium between these openings forms the papillae of the calyx already mentioned. Upon leaving the calyx, the ovarioles seem to lead away at a sharp angle, thus explaining the difficulty found in obtaining both parts in a single section.

The calyx lumen is clear, elongate, and usually cylindrical in the virgin queen. It is often arched in the long dimension, more or less irregularly cylindrical, and loosely filled with detritus in the functional queen (fig. 12).

The debris in the lumen of the calyx possibly consists in part of remnants of follicular and nurse cells from the preceding ovulation (figs. 9, 12). Some of it is so definitely like threads, or sectioned sheets, that it suggests another origin. It varies in appearance, possibly in part owing to histological treatment but more plausibly to the length of time it has been retained in the lumen. It seems to undergo dissolution from a reticular network through a series of changes until it finally becomes a diffuse granular mass. Portions of it are constantly passing down into the upper end of the oviduct and sometimes, when the strands or threads are broken, give the illusion that a thin, squamous cell layer with very



FIGS. 1–9. (See opposite page.)

black nuclei lines the lumen. Apparently it is rather rapidly resorbed from the upper end of the oviduct, for none seems to migrate beyond the narrowed portion of the latter.

The size of the calyx lumen varies in different queens, possibly because of individual variation. Most certainly, its greatest dimensions coincide with ovulation; its smallest, some time afterward. Three were measured, with the following results: Queen '45 L, *E. rogeri,* 1.92 by 0.715 mm.; Queen '45 A, *E. burchelli,* 2.20 by 0.605 mm.; Queen '45 N, *E. hamatum,* 3.30 by 1.100 mm. The last queen was in a physogastric condition. (For initial data on these queens, see Schneirla, 1947, pp. 4–6.)

THE OVARIOLE: The contents of the ovariole passing down the lumen will be considered in part 3 of this series of papers. Here the discussion is limited to the structure of the wall of this part of the reproductive system.

The internal layer of the ovariole is the tunica propria, a structureless membrane. It is quite thin and becomes extremely delicate when large oöcytes distend the ovariole. Outside the tunica, away from the lumen, a single layer of squamous cells invests the ovariole as an epithelial sheath. It is readily seen over the ovarioles of virgin queens but is less conspicuous in the functional, older queen.

The pedicel unites the ovariole with the calyx, and it is in reality

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FIGS. 1–3. *Eciton hamatum.* 1. Junction of vagina and spermathecal duct, sagittal section (H-12). 2. Median oviduct of virgin queen, cross section (H-12). 3. Paired oviduct, proximal end, cross section (PH-3).

FIG. 4. *Eciton rogeri.* Upper flat portion of paired oviduct near calyx, oblique longitudinal section (L).

FIG. 5. *Eciton burchelli.* Spermathecal wall of mature queen (A).

FIG. 6. *Eciton hamatum.* Spermathecal duct and vagina in posterior end of abdomen anterior to their junction; powerful oblique muscles indicated; dorsal abdominal region omitted; cross section of abdomen (PH-3).

FIG. 7. *Eciton rogeri.* Spermathecal duct, cross section (L).

FIG. 8. *Eciton hamatum.* Proximal ends of ovarioles and calyx epithelium of virgin queen before epithelial papillae have formed, sagittal section (H-12).

FIG. 9. *Eciton burchelli.* Proximal ends of ovarioles, calyx wall and papillae formed by its epithelium in mature queen, sagittal section ('44 A).

Abbreviations: bc, bursa copulatrix of vagina; bm, basement membrane; cm, circular muscles; cu, cuticula; dc, debris in calyx; dm, dilator, or retractile muscle; ep, epithelium; ex, exocuticula; fb, fat body; fw, preovulation cells; lp, lumen of pedicel; lpo, possible opening of pedicel into calyx; lu, lumen; luc, calyx lumen; m, muscle; nc, nucleus of calyx epithelium; nf, old follicular nucleus; ns, nucleus of epithelial sheath of ovariole; p, papilla formed of calyx epithelium; sd, spermathecal duct; tg, internal terminal cuticular arch of ovipositor; tm, transverse muscle; tp, tunica propria; va, valve; vag, vagina; vf, vaginal fold; vu, vulva; w, epithelial wall of pedicel.

derived from the calyx epithelium. Its wall is cellular bordering the lumen, and this epithelium seals the lumen of the distal end of the pedicel from that of the ovariole (fig. 8). Regardless of how pleated the lower end of the ovariole may become at times in the functional queen, the lumen of the pedicel is always a smoothly lined, almost straight cylinder. In the illustration (fig. 8) the ovariole of the virgin queen shows most unusual cells, which are here termed preovulation cells, just above the pedicel. Figure 9 of the same material from a functional queen, of course, shows only a pleated ovariole. The wall of the pedicel (fig. 8) is present in three different aspects in one of the ovarioles drawn, a fact due entirely to orientation and the section selected for drawing to reveal other features.

The vitellarium is very long and has the same appearance and size as the pedicel most of the time. It is distended around each oöcyte when the latter is enlarging. Between such oöcytes it pinches in more or less to a smaller diameter depending upon the size of the nurse cell bodies which alternate with the oöcytes in linear position. At times the nurse cell distention is much larger than the area occupied by the young oöcyte.

The wall of the vitellarium is stretched and smooth except for its beaded appearance when filled with oöcytes. When empty, however, the proximal portion is very much shortened by being thrown into accordion-like pleats or folds (fig. 9). The lumen of the pleated ovariole always contains remnants of the nurse and follicle cells from the preceding ovulation just as was mentioned for the calyx. Here, however, the disintegrating nuclei and cytoplasm are in earlier stages of the process.

The germarium is also elongate and always filled with small, mostly undifferentiated cells. Some at the lower end often show mitotic figures. The distal end of the germarium narrows as it joins the terminal filament.

The terminal filament is slender and very elongate. Its axis is filled with a column of transversely placed compacted cells that are no doubt of mesodermal origin, derived from the early gonad. The tunica and mesothelial cellular sheath typical of the rest of the ovariole are conspicuous here.

THE SPERMATHECAL DUCT: The origin of this duct is on the dorsal wall of the vagina just distal to the area that is mentioned as probably the copulatory portion of that organ (figs. 1, 6). The spermathecal duct arises at an acute angle to the vagina and is at first very closely associated with its dorsal wall.

As the duct continues anteriorly in the body, it usually lies directly over the vagina and the median oviduct. In this area it is flatly oval in sectional view; farther anteriorly and indeed for most of its great length it is always cylindrical.

Just behind the origin of the duct, a vertical depression forms a deep ring into which the cuticular intima dips as it follows the contour of the wall. This ring is thought to be the valve regulating the discharge of spermatozoa into the vagina (fig. 1). The muscles are quite prominent and arranged as are those of the vagina except they seem to occur at a slightly more oblique angle at the valve. Almost all of them are ventrally situated (fig. 6). The surface epithelium is largely replaced along this portion of the duct, too, by the muscle insertions. The muscles appear to be dilators and retractors in function.

The cuticular intima is very thick throughout the length of the duct but thinner at the spermathecal junction (figs. 7, 15A–G). Setae of varying degrees of length and thickness protrude into the lumen until the duct reaches the anterior, ventral side of the spermatheca. Often a dark secretion fills the proximal portion of the lumen.

The duct appears to be very smooth and cylindrical in external surface view. The only exception to its roundness is the proximal portion which has already been described as oval in transverse section. After the very thick cuticular layer surrounding the lumen is seen, one can understand why it may be quite impossible for the duct to collapse or kink despite its tight coils and sharp bends (see part 1). A portion of the wall is shown in figure 7. While there are vertical clefts in the intima, they are not represented in the drawings because they are thought to be artifacts due to manipulation. They never reach the surface of the intima. The cuticle of the duct shows no horizontal striations as it does in the spermatheca, but the surface, next to the lumen, is denser than most of the cuticula present below.

Except near the origin of the duct, a single layer of cuboidal cells lies beneath the cuticular intima. The cytoplasm is homogeneous, and no cellular membranes are visible to mark lateral cell boundaries. The cells rest on a basement membrane. The nuclei are oval but appear somewhat longer and larger in cross section than in longitudinal section, no doubt owing to their orientation. Chromatin granules are sparsely present and are frequently peripheral.

The external surface of the duct (away from the lumen) is covered by a layer of circular muscles with small ovate or elongate nuclei that stain darkly. These muscles probably are most important in initiating peristaltic contractions, thus passing sperm down the duct. Usually the muscles seem to consist of one to three cells in thickness. The duct is often separated from the basement membrane by clear spaces.

The distal end of the duct is modified by being enlarged into a reservoir or chamber before opening into the spermatheca. The reservoir is lined with a thin but very dense cuticular layer (figs. 15I–N, 17). Its internal

diameter is approximately three times the size of the duct throughout its length. It is about three times longer than wide and constricts abruptly to join the main portion of the duct. Its terminal opening into the

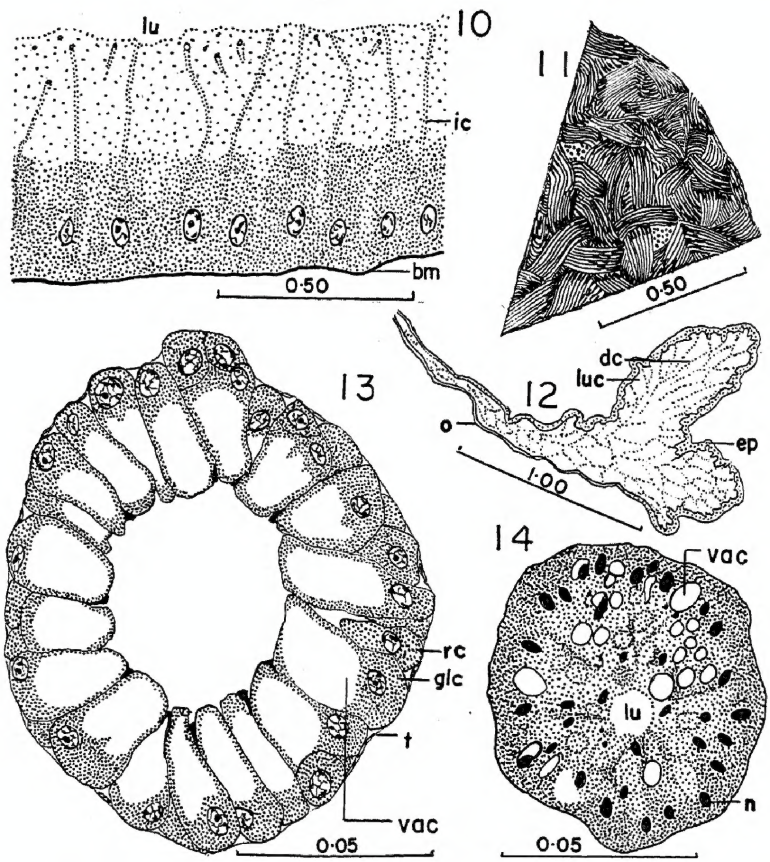


FIG. 10. *Eciton hamatum.* Wall of spermathecal gland, longitudinal section (H-12).

FIG. 11. *Eciton burchelli.* Orientation of spermatozoa in spermatheca (PH-3).

FIG. 12. *Eciton rogeri.* Calyx in cross section and upper end of oviduct in longitudinal section (L).

FIGS. 13, 14. *Eciton hamatum.* 13. Accessory left "lubricating" gland, cross section (H-12). 14. Accessory right "sting" gland, cross section (H-12).

Abbreviations: bm, basement membrane; dc, debris in calyx; ep, epithelium; lu, lumen; luc, calyx lumen; n, nucleus; rc, replacement cell; t, tunica; vac, vacuole.

spermatheca is discussed below, after the spermathecal glands are treated.

THE SPERMATHECA: The wall of the spermatheca is always well rounded to full dimensions when spermatozoa are stored within the organ. Only virgin queens have no spermatozoa, and their spermatheca is in-

variably collapsed. However, such a spermatheca contains an appreciable mass of coarse globules, part of which seem to stain quite dark while the remainder are light. They are not of a fatty nature, for fat-solvent reagents do not affect them. They are absent from the spermatheca of the functional queen.

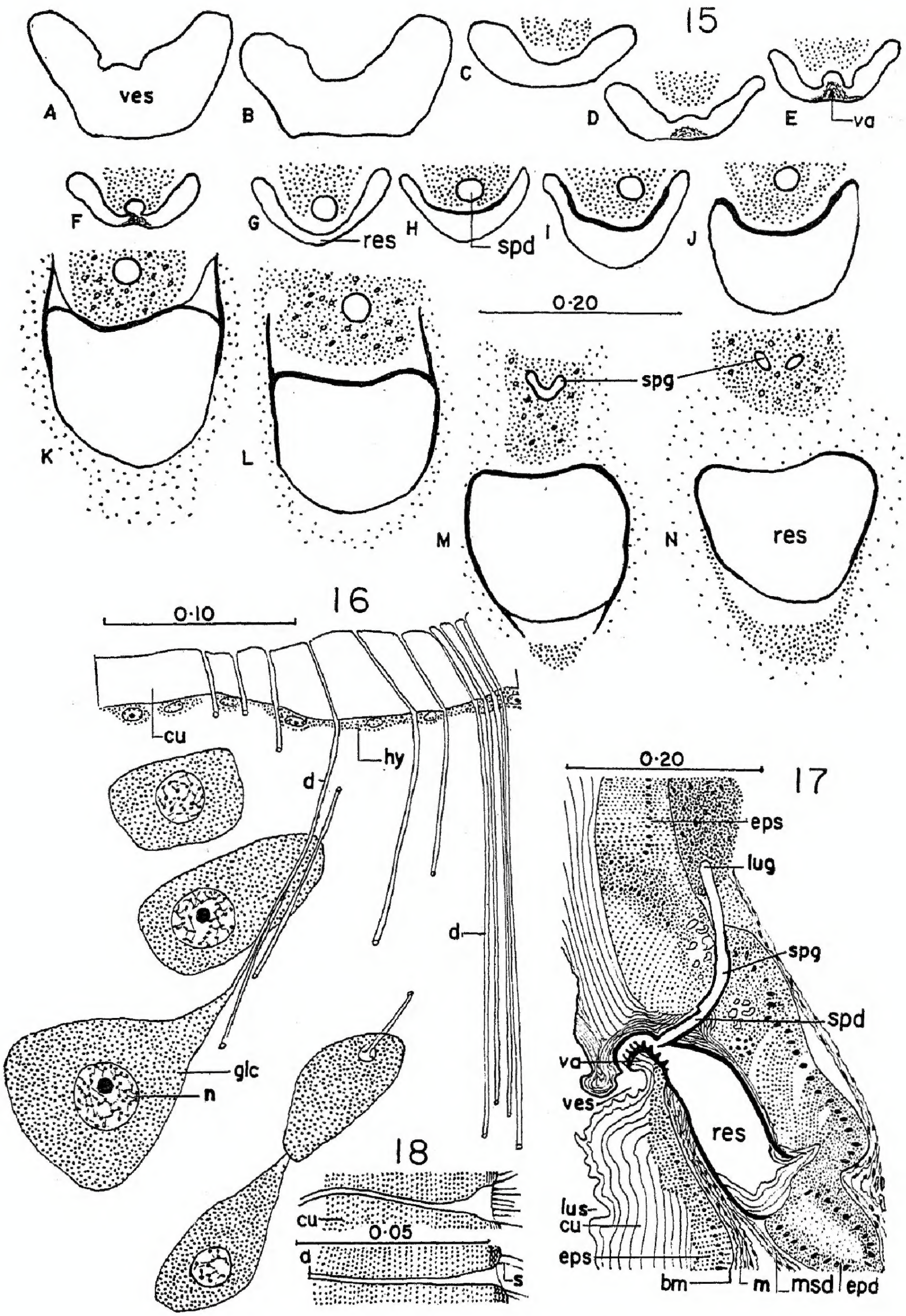
When viewed from the surface, the spermatheca shows a very heavy musculature. The muscles are gathered into thick cylindrical strands, each strand distinctly spaced from the others. They run parallel to one another around the spermatheca, and their contraction would plainly compress the organ and its contents. The latter may thus be forced from the spermatheca into the exit duct in any required volume.

A section of the spermathecal wall reveals each muscle bundle to be several fibers in thickness (fig. 5). Oval spaces without muscles, or with little muscle, exist at intervals over the surface with the epithelium beneath being somewhat more exposed to the surface. The epithelium does not bulge out at these intervals, only spaces between muscles being seen.

Beneath the muscle layer is a single row of exceedingly tall columnar epithelial cells. Each cell is very narrow and rests on a conspicuous basement membrane. The small oval nuclei are set at a definite elevation in the cells, so that all together they form a well-defined row of organelles (fig. 5). Since the cells vary in length, however, the free border of the epithelium is quite wavy in outline. The free margin of the cells would be very indistinct were it not for the cuticular intima secreted by them.

The cuticular layer continues to build up to a considerable thickness in the form of a stratified series of thin sheets. These are wavy in section but in general run parallel over the epithelial surface. At intervals, however, the outer strata seem to surround, or stop at, small knobs or rounded elevations protruding slightly into the lumen. This may be due to partial contraction of the walls of the organ. One may count from 21 to 27 such laminations in the cuticle either in the functional queen of the colony or in the virgin queen. Functional age, apparently, has nothing to do with the depth of this layer. However, the columnar epithelium in the spermatheca of the virgin queen seems to vary from that of the fecund female. Queens '48 H-27 and '48 H-12 are virgins (Schneirla and Brown, 1950). Their spermathecal epithelium is neither so tall nor shows so wavy a free margin as is possessed by the functional queen. It was noted in these specimens, too, that the cuticle showed the number of striations much more clearly, although this effect may be due to technique or staining reaction.

The colony queen always seems to have the spermatheca filled with spermatozoa even though she must certainly use vast numbers of them



FIGS. 15–18. (See opposite page.)

in each statary phase when depositing her eggs. The spermatozoa occur in groups or clumps in the spermatheca with the result that whole clusters appear to be oriented independently of adjacent masses (fig. 11). The individual spermatozoon is very elongate, with a spindle-shaped head. Many hundreds of thousands, perhaps millions, must be contained within the spermatheca. In the figure referred to above, only a suggestion is given of the number of spermatozoa actually present and their arrangement. These points might be better appreciated if one imagines each line in the drawing represents about 100 actual spermatozoa.

Only two ducts open from the spermatheca; one branches and connects with the paired spermathecal glands, the other is the spermathecal duct that leads to the vaginal wall. These ducts join the spermatheca together, and the latter possesses a peculiar, flat, and narrow vestibule for their reception on its anterodorsal surface (fig. 17).

The spermathecal vestibule consists essentially of an opening through the thick cuticular intima lining the lumen and through the epithelium. The opening is slit-like and very much wider than tall. It curves dorsally for half its length, then a reversed curve in its distal half runs anteroventrally through a gap in the epithelium of the spermatheca (fig. 17). Throughout its course, the dorsal wall is smooth, but the ventral wall is not. The first half of the latter is ridged. In the recurved distal half, the cuticle in the center of the ventral floor protrudes as a toothed shelf or valve. Spermathecal epithelium and muscles are present at the base of this valve or shelf. If the muscles are capable of exerting movement in this protruding shelf, the latter could certainly serve as a valve to close the orifice leading into the ducts. Or it could, by its movement, force

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FIGS. 15, 16. *Eciton hamatum.* 15. Spermathecal vestibule, common duct of spermathecal glands, and reservoir of spermathecal duct in successive serial oblique sections cut almost parallel to spermathecal wall in plane at right angle to that shown in figure 17. Dense cuticula indicated by heavy line, lower layers omitted; presence of epithelia and muscles represented by stippling (HD-1). 16. Gland cells of hypodermis (PH-3).

FIG. 17. *Eciton burchelli.* Spermathecal vestibule, common duct of spermathecal glands, and reservoir of spermathecal duct, all in sagittal section (A).

FIG. 18. *Eciton hamatum.* Ductule of hypodermal gland cell traversing exoskeleton which is represented by stippling and the denser surface layers by lines (PH-3).

Abbreviations: bm, basement membrane; cu, cuticula; d, ductule; epd, epithelium of spermathecal duct; eps, epithelium of spermatheca; glc, gland cell; hy, hypodermis; lug, lumen of spermathecal gland; lus, lumen of spermatheca; m, spermathecal muscle; msd, spermathecal duct muscle; n, nucleus; res, reservoir; s, seta; spd, common duct of spermathecal glands; spg, paired duct of spermathecal glands; va, valve; ves, vestibule.

spermatozoa out from the spermatheca. The relation of the vestibule to the adjoining ducts is discussed below.

THE SPERMATHECAL GLANDS: These are very elongate, simple tubular glands consisting of a single pair originating on the anterodorsal surface of the spermatheca. The main portion of each gland lies in loose irregular coils beneath the spermatheca and may often extend anterior to it in the ventral fat body tissue. As their proximal ends approach the spermatheca they pass upward along the latter's anterior or anterolateral surface, then bend towards the midline. Here they fuse to form a common duct leading through the spermathecal wall. The common duct contains not only an intima but an outer thick layer of circular muscles.

Sections through the spermathecal gland show an outer heavy basement membrane supporting a single layer of very tall, pyramidal secretory cells with ovate, basally situated nuclei (fig. 10). These cells stain strongly and usually differentially. The basal third or half of each cell is generally quite overstained, while the central and distal portions are light in color. However, when secretory activity is great there is also an accumulation of darkly stained products at the free margin of the cell next to the lumen. At such times only the central area of the cell is light. Sometimes a lighter vacuole, about the size and shape of the nucleus, may be seen in the basal portion of the cell. Cell membranes along the sides and free ends of the cells are indistinct, and the lumen of the duct, compared with the thickness of its wall, is proportionately very small.

Intracellular canals are characteristic of these cells, and they are long and conspicuous. They stain very dark or even black. Their distal ends discharge through a distinct pore into the lumen of the duct. If the canals are cut transversely they appear as dark rings or black discs according to their state of activity in carrying secretions.

RELATIONS BETWEEN SPERMATHECA AND ITS DUCTS: Students of the Hymenoptera seem to be of the opinion that, in the ants, the duct of the spermathecal glands unites with the spermathecal duct and not with the spermatheca. Two especially favorable series of sections of the junction of these parts in the army-ant queen enable us to examine the conditions as they appear to exist in this insect (figs. 15, 17).

The vestibule of the spermatheca and the reservoir of the spermathecal duct are briefly described above. The paired spermathecal glands possess individual ducts which penetrate the spermathecal musculature and epithelium. At first these ducts within the spermathecal tissue are directed anteriorly almost parallel to the spermathecal wall. They also approach one another at the same time and fuse to form a common spermathecal gland duct. This common duct is formed within the spermathecal epi-

thelium almost at the free (distal) margins of the epithelial cells between which it passes. The common duct pursues a course almost directly ventrally in the spermathecal wall, and most of it lies embedded in what appears to be spermathecal cuticula (fig. 17). This conclusion is reached because spermathecal epithelium surrounds the paired ducts and the base of the common duct although it appears to be considerably displaced in providing space for passage of the duct. The less dense cuticle anterior to the common duct (below in the figure) is thought to be derived from the spermathecal epithelium beneath it. All cuticle in figure 17 is represented in parallel wavy lines, and its relative density is indicated by width of lines and their spacing.

The spermathecal duct penetrates the spermathecal musculature in a posterior direction with relation to both general body direction and the orientation of the spermatheca. A parasagittal section of its wall is shown in the lower right of figure 17. Upon reaching the epithelium, the distal end of the spermathecal duct enlarges into a reservoir. The latter possesses its own ventral musculature which probably dilates the organ at appropriate times. Ventral to the reservoir and its muscles lie spermathecal muscles, epithelium, and cuticula. The spermathecal epithelium is much shorter in height than elsewhere over the spermathecal wall, but the muscular layer is relatively thick. These two tissues stop at the base of the valve of the vestibule, but the valve is composed of spermathecal cuticle.

The proximal opening of the common duct of the spermathecal glands and the proximal opening of the reservoir both discharge through spermathecal cuticle into the vestibule of the spermatheca. If the shelf or valve of the vestibule is movable when the adjacent spermathecal muscles contract, it is entirely possible one, or both, of these openings will be closed. If the ventral muscles of the reservoir contract, this organ could be expanded in size, thus drawing in a supply of secretion from the spermathecal gland duct. It should also be stated that in several specimens spermatozoa were found in the vestibule and the common duct of the spermathecal glands.

Figure 15 shows the distal half of the vestibule in a series of successive sections to reveal this structure and its valve in another aspect that its dimensions may be more fully appreciated. The sections are cut almost parallel to the outer surface of the spermatheca, hence the reservoir in the later outlines of the series is proportionately too large. It is cut almost in an oblique plane.

The preceding explanation and the illustrations have led to the conclusion that in the army-ant queens subject to this study the common

duct of the spermathecal glands and the spermathecal duct open independently into the distal end of the spermathecal vestibule. However, it is entirely possible that the vestibular valve and muscles of the reservoir may regulate the amount and direction of movement of both spermatozoa and glandular secretions.

THE ACCESSORY GLANDS: The right gland of this pair has been assumed to be the poison gland of other authors on the Hymenoptera (fig. 14). A limiting membrane is present on its exterior surface, and within this are the secretory cells. The tissue is two or three cells in thickness, but cell membranes do not separate them from one another for the observer. The cytoplasm contains numerous vacuoles of various sizes. It is densely granular, and these granules take the nuclear stain which makes them very dark. At certain times the granules are rather regularly distributed throughout the tissue; at intervals they seem to aggregate towards the periphery of the gland.

The nuclei are not unusual in size but stain so heavily the internal disposition of the chromioles and linin was not seen in the present sections; they are represented in black. The lumen of the duct is small.

The left gland, said to have a lubricating function, varies greatly from its mate. An external membrane also surrounds the secreting cells, but it is a more delicate structure. The cells are arranged in a layer, one cell in thickness, around a large lumen. Between the active cells and the limiting membrane one can find an occasional, smaller replacing cell (fig. 13). The active cells are very large, and each contains a single huge vacuole, possibly containing a serous or mucoid secretion. The cytoplasm of each cell surrounds its vacuole, but most of it accumulates basally.

The nuclei are large, with linin and peripherally distributed chromioles clearly visible. The cell borders surrounding the lumen often project slightly into the latter so the outline in cross section is irregular. Between the projecting ends of the cells some denser secretion in the lumen frequently lodges.

THE HYPODERMAL GLAND CELLS: Not directly connected with the reproductive system are two pairs of glandular cell masses, segmentally arranged, in the vicinity of the vulva. They are included because it is possible their secretions may influence the behavior of the members of the colony in their relations with the queen. Each glandular mass consists of approximately 50 cells (fig. 16).

The cells are generally pear-shaped, but the marginal cells are often ovate in contour. Each is a unicellular gland and possesses its own individual ductule leading from the cytosome to the external hypodermis. This ductule stains quite black but shows a clear lumen within a fairly

thick wall. Upon reaching the outer border of the hypodermis, the ductule seems to continue through the cuticular exoskeleton almost onto the external surface of the insect.

It is possible that the cytoplasmic ductule extends through the exoskeleton because there is no break, constriction, or discontinuity visible in its wall or lumen. In some preparations the heavy staining reaction ceases abruptly at the hypodermal surface; in others it continues to the external cuticular surface. The ductule is approximately the same diameter throughout its length but enlarges at its point of external discharge (fig. 18). No evidence of cytoplasmic tissue is visible in the expanded external opening.

While the wall surrounding the lumen of the ductule is quite smooth and uniform throughout its course in the cuticle, the latter appears to be clearly influenced by its passage. The cuticle is laminated and shows wavy horizontal lines bordering each secreted sheet. Each sheet is interrupted where the ductule passes through, and the border of the lamination against the side of the ductule is easily seen as a curved half-circle, for only half of the perforation can be seen at the focal point under high power. The same illusion could be easily produced if a colored tube were seen slightly obliquely as it passes through several closely appressed clear plastic sheets.

The cytoplasmic ductule appears on the slide to originate in two slightly different ways, but this effect may be due to an optical illusion or to the orientation of the cell when viewed. In one case the pear-shaped cell exhibits an elongate, cone-like taper which gradually narrows into the ductule. In the other example, the cone-like origin of the duct is very short and seems to arise abruptly from the smoothly curving cell surface. Both are represented on the drawing (fig. 16). The lumen of the ductule is not only quite clear but sometimes refractive. The elongated tapering cone leading from the cell and forming the ductule is also clear at its distal end.

The gland cell is enormous, as one can see in comparing it in size with the hypodermal cells above. The cytoplasm is densely and coarsely granular, and the cell membrane is conspicuous. The nuclear membrane is likewise quite evident and surrounds a very large nucleus. The nucleoplasm is clear but contains a multitude of small chromioles distributed on linin. A single spherical nucleolus is often subcentrally situated in the nucleus.

While some of the cells lie close to the hypodermis, most of them extend more deeply into the haemolymph. Their ducts consequently are considerably more elongate in such cases. They are closely aggregated

but not compressed together, so each cell generally maintains its ovate or, most typically, pear shape. No fat cells are associated with them, but usually a few are visible close by.

It is quite possible more of these glands are present in other segments, but only the two pairs were observed. These glands, or their homologues, may be possessed by the worker caste. It has been assumed by Santschi (1911) and Schneirla (1933) that workers may press their gaster to the ground in order to exude a glandular secretion onto the substratum. The presumed chemical trail serves to guide other members of the colony. The queen, however, is never in a position to utilize these glands for similar purposes. She is always attended by numbers of workers who exhibit every evidence of a marked responsiveness to secretions from the glands she possesses. It is probable that their reactions to her secretions are quite different from those to the glandular secretions of workers, and a chemotactic basis for such discrimination has been suggested by Schneirla and Brown (1950). The probability has been discussed by Schneirla (1953) that slight differences in the secretions of callow queens and a more intense characteristic secretion in the adult functional queen influence the differential responses of attendant workers and play a basic role in colony division.

In the past, students of army ants have assumed that some attractant prompted the licking of the gaster of the queen and the solicitude afforded her by the workers. None knew the source of such attentions but supposed it originated somewhere on the gaster or was emitted from the vulva. The discovery and description of these glands provide the first adequate physical evidence that attractants may exist as exudations, for these glands are definitely secretory in function and open upon the external surface of the gaster. These facts, however, do not prove the chemotactic behavior of workers and the secretion from the glands are definitely linked. They may have any one, or more, of several functions in the economy of the queen and the colony, and experimentation as well as observation must determine what they are. At any rate, a physical basis for intensive concentration on glandular secretions in queenly behavior and colony activity has now been established. A chemotactic function is, naturally, the first possibility the myrmecologist has in mind.

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